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Large seeds provide an intrinsic growth advantage that depends on leaf traits and root allocation

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Abstract

1. Seed mass and growth rate are important dimensions of plant ecological diversity, but their relationship remains unresolved. Negative relationships between RGR and seed mass are well-established. However, RGR is size dependent, so small-seeded species might achieve fast growth simply because they are initially small.
2. Using a dataset of unprecedented size, sampling 382 grass species, we investigated seed mass and growth rate using both RGR and SGR (RGR at a specific size), accounting for diversity in phylogeny, ecology (e.g. life history, photosynthetic pathway) and environment (mean annual temperature and precipitation).
3. RGR and SGR showed contrasting relationships with seed mass, such that large-seeded species had lower RGR but higher SGR than small-seeded species. However, the relationship between SGR and seed mass depended on leaf dry matter content (LDMC), and was only positive in high-LDMC species. When compared at a common size, the fast growth of large-seeded and low-LDMC species was associated with greater biomass allocation to roots in the hot, high-light environment used for our experiment. Photosynthetic pathway and life history contributed to variation in SGR, with C_4 annuals having higher SGRs than C_3 perennials regardless of seed size.
4. Large seeds therefore afford an intrinsic growth advantage in species with resource-conserving leaf traits, and may provide a competitive edge in resource-poor environments. This work advances the understanding of how seed mass and growth rate co-evolve with other ecological factors.

KEYWORDS

grasses, growth rate, leaf dry matter content, leaf mass ratio, Poaceae, root mass ratio, seed size, specific leaf area

1 | INTRODUCTION

The seed mass and growth rate of plants influence a number of important ecological processes including establishment, competition, stress tolerance and resilience to disturbance (Grime & Hunt, 1975; Metz et al., 2010; Pacala & Rees, 1998; Tilman, 1994; Turnbull et al., 1999; Westoby, 1998) and, as such, are used to differentiate species by their ecological strategy (e.g. the r–K continuum; Gadgil & Solbrig, 1972). Despite their importance in ecology, the relationship between these traits is unresolved. This relationship has been a research focus for 30–40 years (e.g. Stebbins, 1976), but work has suffered from methodological shortcomings, resulting in inconsistent and often contradictory findings.

A negative relationship between seed mass and the typical measure of plant growth efficiency, RGR, has been documented widely (e.g. Baraloto & Forget, 2007; Maranon & Grubb, 1993; Poorter et al., 2008). However, RGR (calculated as the log of the ratio of final to initial size divided by the duration of the study) suffers from one major problem—it is not independent of size (Poorter & Remkes, 1990; Reich et al., 2002). RGR assumes exponential growth but most organisms become increasingly inefficient as they grow due to self-shading, tissue turnover and allocation to structural components (Enquist et al., 1999; Maranon & Grubb, 1993). This size dependency means that RGR values are at least partly determined by initial size, making the comparison of species with different initial sizes (i.e. different seed masses) particularly problematic. All else being equal, small-seeded species should exhibit a higher RGR than larger seeded species by virtue of their small initial seedling size. Thus, the well-supported negative relationship between seed mass and RGR—considered almost a truism in plant ecology—may arise from differences in seed mass alone, and no other aspect of plant biology (Turnbull et al., 2012).

In response to the size dependency of RGR, an approach was developed to calculate RGR at a standard size—SGR—(Rees et al., 2010; Rose et al., 2009; Turnbull et al., 2008). By fitting species-specific growth curves and extracting RGR values at a common reference size, SGR more closely reflects the intrinsic growth capacity of species. The use of SGR has built in momentum over the past decade (e.g. Paul-Victor et al., 2010; Zust et al., 2011), and when SGR has been explored in relation to seed mass, starkly contrasting relationships have been found in comparison to those with RGR. For example, Turnbull et al. (2012) found, across 10 diverse datasets, that while the slope of the relationship between RGR and seed mass was consistently negative, the slope of the seed mass versus SGR relationship varied widely and was often positive. More recent studies have found similarly inconsistent results (e.g. Philipson et al., 2014), and thus, the relationship between seed mass and growth rate remains unclear.

Why might growth rate depend upon seed size across species when they are compared at a common size? It has been hypothesised that different-sized seeds have unequal energy reserves, which impacts on seedling growth (Baskin & Baskin, 2014; Donohue, 2009). However, given the short duration of seed reserve effects, this seems unlikely to explain variation in growth rate when plants are compared at different ages but at a common size, particularly in resource-rich environments. Alternatively, differences in plant functional traits and allocation of biomass associated with seed size may explain interspecific growth rate variation when compared at a common size. For example, a greater biomass investment in roots in large-seeded species has been observed in multiple plant groups (Baker, 1972; Buckley, 1982; Lloret et al., 1999). Likewise, seed mass is known to correlate with functional traits that may influence RGR, such as SLA and leaf dry matter content (LDMC; Maranon & Grubb, 1993; Philipson et al., 2014). Such associations may indirectly lead to growth differences between species associated with seed size.

To gain insights into the elusive seed mass versus growth rate relationship and its underlying causes, we analyse an exceptionally large dataset of traits from grasses grown under common environmental conditions within a phylogenetic and ecological framework. Furthermore, eliminating growth rate size dependency issues by using SGR, our study overcomes several other methodological shortfalls of previous studies. We explore the relationship between seed mass and growth rate in 382 grass species—a species sample more than an order of magnitude larger than in any previous study (Ben-Hur & Kadmon, 2015; Maranon & Grubb, 1993; Paul-Victor et al., 2010; Taylor et al., 2010). With strong phylogenetic signals in both seed size and plant growth rate (Atkinson et al., 2016; Moles et al., 2005), ancestry may play a role in causing seed mass versus growth rate relationships. Therefore, unlike the majority of previous studies, we incorporate a phylogeny of the study species into our analyses to account for evolutionary history. Finally, ecological factors that influence seed mass and/or growth rate should be accounted for when exploring the relationship between these traits (Table 1). The large species sample allows us to incorporate information on physiology, morphology, life history and climatic niche into analyses, allowing us to test whether seed size effects depend on other functional traits. We predict that large seed sizes will result in faster growth compared with smaller seeded species, but that this positive relationship will only be uncovered when using the size-corrected method, SGR. In the high-light environment of our experiment, water and nutrient availability will have a greater impact than light in determining growth rate. Therefore, if seed size correlates with below-ground biomass investment, such limitations should impact on the growth of small-seeded species to a greater extent than that of large-seeded species.

2 | MATERIALS AND METHODS

2.1 | Seed mass and plant growth data

Detailed methodology on experimental design, seed preparation and plant growth modelling can be found in the study by Atkinson et al. (2016). Briefly, seeds of 382 grass species, representing a broad sample across the two grass family (Poaceae) clades

TABLE 1 Ecological and climatic traits and their expected associations with plant growth rate and/or seed mass

Trait	Relationship with growth rate	Relationship with seed mass
Domestication status	Domesticated grasses do not grow faster than wild species (Evans, 1993; Simpson et al., 2017)	Domesticated grasses and their progenitors have higher seed masses than wild species (Cunniff et al., 2014; Preece et al., 2017)
Growth form	Consistent differences exist between growth forms (e.g. Houghton et al., 2013). In grasses, rhizomatous/stoloniferous species may have relatively high growth rates, due to lower self-shading	Growth form contributes to variation in seed mass (Moles et al., 2007; Rees, 1996)
Leaf dry matter content	LDMC correlates negatively with potential RGR (Simpson et al., 2020; Wilson et al., 1999)	Seed mass is negatively related to SLA (Maranon & Grubb, 1993; Philipson et al., 2014), which implies a positive relationship with LDMC (LDMC tends to scale with 1/SLA)
Life history	Growth rate is higher in annuals than in perennials (Garnier, 1992)	Seed mass is positively correlated with plant longevity (Hodkinson et al., 1998; Rees, 1996)
Mean annual precipitation	Growth rate in grasses is independent of mean annual precipitation (Atkinson et al., 2016)	Large-seeded species can establish in drier environments than small-seeded species (Daws et al., 2008; Metz et al., 2010; but see Murray et al., 2004)
Mean annual temperature	Growth rate in grasses is independent of mean annual temperature (Atkinson et al., 2016)	Seed mass is positively correlated with temperature (Moles et al., 2005)
Photosynthetic pathway	C_4 photosynthesis causes a daily growth enhancement in grasses (Atkinson et al., 2016; Simpson et al., 2020)	C_4 grass seeds have a lower mass than C_3 grass species (Csontos & Kalapos, 2013)

(BOP (Bambusoideae, Oryzoideae and Pooideae) and PACMAD (Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae and Danthonioideae)), were obtained, their pericarps removed and 10 air-dried seeds per species weighed using a four-point balance to calculate an average mass. Twenty seeds of each species were sterilised and germinated, and seedlings were transplanted into 1-L tubular pots (length, 5 cm; width, 5 cm; height, 40 cm; containing 90% vermiculite and 10% sand by volume). Plants were grown in a controlled environment chamber (MTPS 120, Conviron) to provide a day/night temperature of 30/25℃, 70% relative humidity, a day length of 14 hr and a maximum photosynthetic photon flux density (PPFD) at canopy height of 1,600 μmol m^{-2} s^{-1}. We aimed for non-limiting water and nutrient availability by watering plants twice daily and fertilising twice weekly.

Plants were harvested weekly for 5 weeks. The harvested material was divided into leaf, stem and root fractions, and the fresh mass of each determined. In addition, the total leaf area (using WinDIAS leaf imaging system, Delta T devices), as well as average root length and diameter (using WinRhizo image analysis system, Régent) were determined for harvested plants. Plant material was then oven-dried and weighed. SLA (leaf area divided by leaf dry mass), leaf mass ratio (LMR; leaf dry mass divided by total plant dry mass), LDMC (dry mass of a leaf divided by its fresh mass), root mass ratio (RMR; root dry mass divided by total plant dry mass) and specific root length (SRL; the ratio of root length to dry mass) were calculated for each individual.

Total plant dry mass over time was used to model species-specific growth curves using the R language and environment (R Core Team, 2019). RGR values were calculated as a linear regression of log(mass) against time for each species. For SGR, a four-parameter logistic model was fitted for each species using the 'nlme' function (Pinheiro et al., 2019). The four parameters A (minimum mass), B (the maximum mass), t_0 (the time when a plant is midway between A and B) and k (a growth parameter) were fitted as independent, species-specific random effects. Using this model (following Rees et al., 2010), the SGR can then be given by:

$$\frac{k(A - \ln(M_c))(B - \ln(M_c))}{(A - B)},$$

where M_c is the mass at which SGR is calculated. A small plant size was chosen to calculate SGR at (the 20th percentile for total plant dry weight across all species and all harvests) since this is when growth rate is expected to be closest to its intrinsic upper limit (Grime & Hunt, 1975).

To determine whether the mass at which we were comparing the growth rate of species influenced the results, additional analyses at two other masses (the 50th percentile and the largest minimum mass of any of the study species (representing a minimum size where all species overlap)) were performed. These produced qualitatively similar results in terms of statistical significance and the direction of the relationship (see Table S1 in Supporting Information).

2.2 | Comparative analyses

To determine the relationship of seed mass with RGR and SGR, we used a phylogeny of the species (Atkinson et al., 2016) and the 'MCMCglmm' function in R (MCMCGLMM package; Hadfield, 2010). This method implements Markov chain Monte Carlo routines for fitting GLMMs, and accounts for non-independence and correlated random affects arising from the phylogenetic relationships. Explanatory variables were fitted based on a priori expectations that they might influence growth and/or seed size (Table 1). Therefore, we accounted for life history (annual or perennial; collated from GrassBase, Clayton et al., 2006), growth form (rhizomatous/stoloniferous or bunch-forming (i.e. caespitose); same source as life history), domestication status (domesticated cultivar or wild; from seed distributor information, otherwise classified as 'wild'), photosynthetic pathway (C_3 or C_4; from Osborne et al., 2014), LDMC (calculated at a common reference size, 20th percentile for total plant dry weight) and two climatic variables (mean annual precipitation, MAP, and mean annual temperature, MAT; see Atkinson et al. (2016) for determination of species values). These variables were fitted as explanatory variables, together with seed mass, in an additive model (i.e. growth.rate ~ seed.mass + LDMC + photosynthetic.pathway + life.history + domestication.status + MAP + MAT). To account for phylogeny, species was included as a random effect. This random effect uses the inverse of a phylogenetic correlation matrix of the study species (see Hadfield and Nakagawa (2010) for a detailed discussion of this approach). Seed mass and LDMC data were log-transformed to improve normality prior to analysis. To test for interactions with seed mass and each other explanatory variable, interaction terms were added to an additive model and any significant interactions were included in the final model. Models were run for 100,000 iterations with a burn-in of 1,000 iterations and a thinning interval of 500 using parameter-expanded priors (Hadfield, 2019). We used the R package VISREG (Breheny & Burchett, 2017) to display the results of these fitted models in terms of how certain predictor variables (LDMC, life history, photosynthetic pathway) are estimated to affect the response variables (SGR or RGR). To do this, we refitted the models (as the visreg command cannot take MCMCglmm models) using the 'gls' function (in the NLME package) with the phylogeny describing the within-group correlation structure in order to make partial residual plots. Refitting with gls produced quantitatively similar model outputs (Table S2).

To test whether variation in seed mass was associated with particular ecological and climatic variables, a MCMCglmm model was fitted, as described above, with seed mass as the response variable. We explored how seed mass correlates with the different components of growth rate. Above-ground RGR variation can be broken down into three components: SLA, LMR and NAR (net assimilation rate; growth rate per unit leaf area; Hunt, 1982). SLA and LMR were estimated at the same common reference size as SGR (20th percentile for total plant dry weight) across the study species (following Rees et al., 2010). Leaf NAR was calculated from these by dividing SGR by the leaf area ratio (the product of SLA and LMR; following Lambers & Poorter, 1992) estimated at a common size. To explore how below-ground allocation might differ between species, root traits equivalent to above-ground RGR components (SRL, RMR and root NAR; the latter calculated as SGR divided by the product of SRL and RMR) were estimated at a common reference size. All components of RGR, except LMR and RMR, were log-transformed prior to analysis.

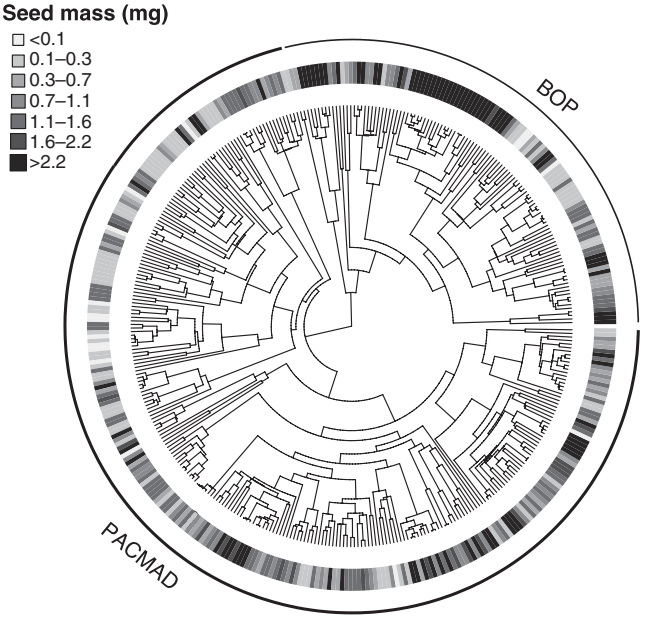

FIGURE 1 The distribution of seed masses across 382 grass species. BOP and PACMAD are the two major grass clades. Seed mass showed a strong phylogenetic signal (Pagel's $\lambda = 0.92$; 95% confidence interval = 0.859–0.952)

We carried out an additional analysis to explore how LDMC influences the relationship between root traits (RMR and SRL) and seed mass. Using the same MCMCglmm approach as before, we modelled the effect of LDMC, seed mass and photosynthetic pathway (the latter was included as it is known to influence both LDMC and RMR in grasses; Atkinson et al., 2016) on RMR and SRL. Significant interactions with the explanatory variables were included in the final analysis.

Marginal R^2 values (i.e. those associated with fixed effects only) for all MCMCglmm models were estimated following Nakagawa and Schielzeth (2013).

3 | RESULTS

Seed mass varied hugely across the 382 grass species studied (Figure 1), with the largest-seeded species (*Zea mays*: 83.2 mg) having an average seed mass almost 300 times greater than the smallest-seeded species (*Thysanolaena latifolia*: 0.28 mg). RGR also varied widely, showing 30-fold variation among species (0.009 (*Dichanthelium leibergii*) versus 0.312 (*Stipagrostis hochstetteriana*) g g^{-1} day^{-1}; Figure S1). However, SGR varied to a much lesser extent, showing only fourfold variation among species (0.075 (*Festuca*

petraea) versus 0.309 (*Sorghum arundinaceum*) g g^{-1} day^{-1}; Figure S1), implying that most of the variation in RGR among species arises from differences in initial size.

3.1 | Seed mass and growth rate

After accounting for diversity in phylogeny, environment and key ecological traits, we found starkly contrasting relationships between seed mass and the two measures of growth rate, RGR and SGR. Using RGR, we found the well-established, significantly negative relationship with seed mass [slope estimate = −0.010 (95% confidence interval (CI): −0.014 to −0.006), $p < 0.001$; Figure 2; Table 2], such that small-seeded species have a growth advantage over large-seeded species. In direct contrast, when growth rate was compared at a common size, SGR was significantly positively related to seed mass [slope estimate = 0.017 (95% CI: 0.007 to 0.028), $p < 0.001$; Figure 2; Table 2]. The only significant interaction between seed mass and the other explanatory variables was that with LDMC in relation to SGR. The effect of seed size on SGR depended upon LDMC [estimate = 0.009 (95% CI: 0.003 to 0.014), $p = 0.002$] such that, for species with low LDMC, seed mass has little effect on SGR. However, for species with high LDMC, there is a positive seed size effect on growth rate (Figure 2).

Above- and below-ground components of growth rate were associated with seed mass (Figure 3; Tables S3 and S4). Large-seeded species invested proportionally less biomass above-ground in leaves (lower LMR; $p < 0.001$) although SLA did not differ with seed size (Figure 3a,b). The larger proportion of biomass allocated below-ground (higher RMR; $p < 0.001$) in the larger seeded species consisted of roots with a lower SRL ($p < 0.001$; Figure 3d,e). In turn, SRL was highly negatively correlated with root diameter (Figure S2), such that large-seeded species had thicker roots with a higher mass per unit length than small-seeded species. Growth rate per unit leaf area (leaf NAR; $p < 0.001$) and per unit root length (root NAR; $p < 0.001$) were both positively related to seed mass (Figure 3c,f).

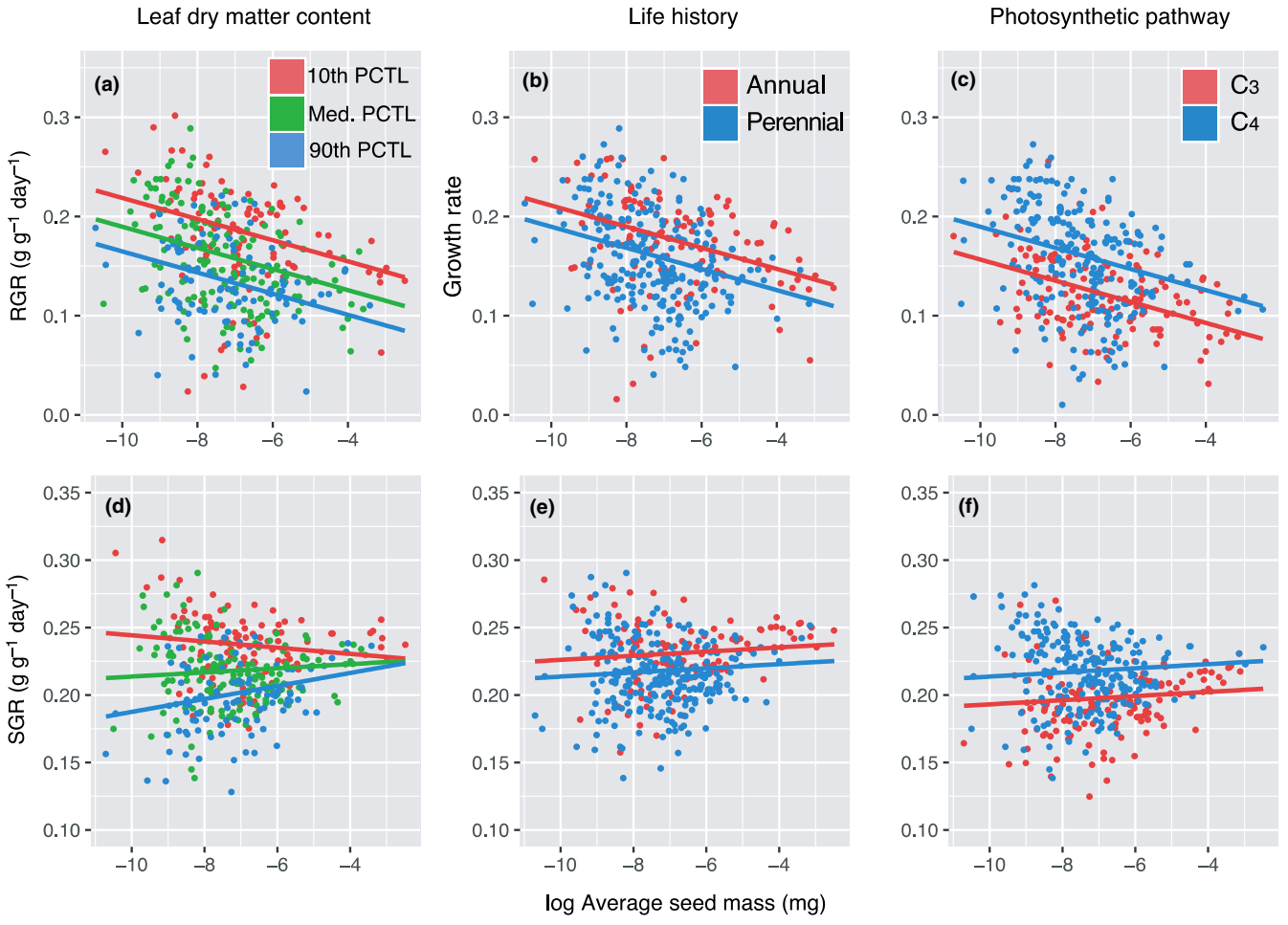

FIGURE 2 Relationships between seed mass and two growth rate measures—RGR (panels a–c) and size-standardised growth rate (SGR; d–f) —across 382 grass species. In each partial residual plot, variation due to other variables is corrected for to enable clearer interpretation of relationships (i.e. variation due to life history and photosynthetic pathway is accounted for in a and d; variation due to leaf dry matter content (LDMC) and photosynthetic pathway are accounted for in b and e, etc.). RGR and SGR are high in low-LDMC (a, d), C_4 (b, e), annual species (c, f) across the range of seed sizes. Lines in a and d are calculated for the 10th, median (med.) and 90th percentile (PCTL) of LDMC. Lines shown are extracted from generalised least square linear models (coefficients given in Table S2)

TABLE 2 The contributions of plant traits and environmental variables to growth rate measures across 382 grass species. Values represent posterior mean estimates of the slopes as determined by MCMC phylogenetic GLMMs, as well as the upper and lower 95% confidence intervals and *p*-values. The explanatory variables could together explain 64% of RGR variation [marginal $R^2 = 0.64$; 95% highest posterior densities (HPD) = 0.416–0.854] and 65% of size-standardised growth rate (SGR) variation (m$R^2 = 0.65$; 95% HPD = 0.471–0.828). Significant model terms ($p < 0.05$) are in bold. CI, confidence interval; '*', $p < 0.05$; '**', $p < 0.01$; '***', $p < 0.001$

	RGR		SGR	
	Estimate (95% CI)	***p*-value**	**Estimate (95% CI)**	***p*-value**
(Intercept)	−0.041 (−0.091 to 0.007)	0.108	0.253 (0.175 to 0.328)	**<0.001** ***
Domestication status (cultivar -> wild)	−0.0003 (−0.017 to 0.017)	0.97	−0.001 (−0.010 to 0.008)	0.80
Growth form (bunch-forming -> stoloniferous/rhizomatous)	0.007 (−0.004 to 0.017)	0.22	0.001 (−0.005 to 0.006)	0.77
Leaf dry matter content	−0.062 (−0.079 to −0.045)	**<0.001****	0.020 (−0.021 to 0.060)	0.32
Life history (annual -> perennial)	−0.024 (−0.036 to −0.012)	**<0.001****	−0.013 (−0.019 to −0.007)	**<0.001****
Mean annual precipitation	9.15e-6 (−3.78e-6 to 2.26e-5)	0.17	6.71e-6 (−5.68e-7 to 1.38e-5)	0.07
Mean annual temperature	1.27e-4 (−7.41e-4 to 9.56e-4)	0.77	4.58e-5 (−0.0004 to 0.0005)	0.85
Photosynthetic pathway (C_3 -> C_4)	0.034 (0.015 to 0.053)	**0.001****	0.023 (0.011 to 0.035)	**<0.001****
Seed mass	−0.010 (−0.014 to −0.006)	**<0.001****	0.017 (0.007 to 0.028)	**<0.001****
Seed mass: Leaf dry matter content			0.009 (0.003 to 0.014)	**0.002****

3.2 | Other trait associations with growth rate

Plant and climatic trait data (seed mass, LDMC, photosynthetic pathway, growth form, MAP, MAT, life history and domestication status) together explained considerable variation in both RGR (marginal $R^2 = 0.64$) and SGR (marginal $R^2 = 0.65$; coefficients listed in Table 2). In addition to seed mass, two traits significantly contributed to all growth rate measures: photosynthetic pathway and life history. Irrespective of seed size, C_4 annual species always had higher growth rate values than C_3 perennials ($p < 0.001$). LDMC was also an important trait—it was significantly negatively associated with RGR ($p < 0.001$). Growth form, domestication status and the two climatic variables (MAP and MAT) never contributed to any measure of growth rate (Table 2). While the influence of these variables on seed mass is well-established (Table 1), their influence on growth rate is smaller or unclear (e.g. grass domestication causes an increase in seed mass but not an increase in growth rate; Evans, 1993; Simpson et al., 2017).

3.3 | Associations between seed, root and leaf traits

A small amount of the variation in seed mass among species could be explained collectively by plant and climate traits (marginal $R^2 = 0.04$; Table S5), with two individual traits, domestication status [estimate = −0.55 (95% CI: −0.88 to −0.22), $p < 0.001$] and MAP [estimate = −3.1e-4 (95% CI: −5.9e-4 to −3.1e-5), $p = 0.024$], having a significant influence, such that cultivated species from drier environments have larger seeds than wild species from wetter environments.

Leaf dry matter content significantly influenced the relationship between root traits (RMR and SRL) and seed size (Figure 4; Figure S3; Table S6). Low-LDMC species tended to have higher root mass ratios [estimate = −0.03 (95% CI: −0.06 to −0.01), $p = 0.023$] and specific root lengths [estimate = −0.21 (95% CI: −0.35 to −0.08), $p = 0.002$], independently of seed size and photosynthetic pathway (i.e. no significant interaction). This meant that the fast growth of low-LDMC species, which occurred independently of seed mass, was associated with high allocation to thinner roots with a lower mass per length. There was a significant interaction, however, between seed size and photosynthetic pathway in relation to RMR ($p = 0.01$; Figure 4) and SRL ($p < 0.001$; Figure S3; Table S6), such that C_4 species had high RMR regardless of seed mass but in C_3 species, RMR was positively associated with seed size. SRL declined more steeply with increasing seed size in C_3 species in comparison to C_4 species.

4 | DISCUSSION

Here we comprehensively address a long-standing debate in the literature by analysing seed mass, growth rate and functional trait data at an unprecedented scale, while accounting for phylogenetic and ecological diversity. We show that growth rate depends on the interacting effects of seed size and leaf construction, when compared across species at a common plant size. Large-seeded species grow fast (high SGR) regardless of their leaf traits, but LDMC determined the seed size effect on growth in small-seeded species. For species with low LDMC, there was no seed mass effect—these species were near their maximum SGR (~0.25 g g^{-1} day^{-1}; i.e. ~25% daily increase in biomass) and could not grow much faster regardless of seed size. However, the opposite was true for species with high LDMC which showed elevated growth rate with increasing seed size. LDMC determines the density and cost of leaf tissue, and is a key trait on the leaf economics spectrum (Grime et al., 1997; Pierce et al., 2013; Ruiz-Robleto & Villar, 2005). Our work therefore shows that seed

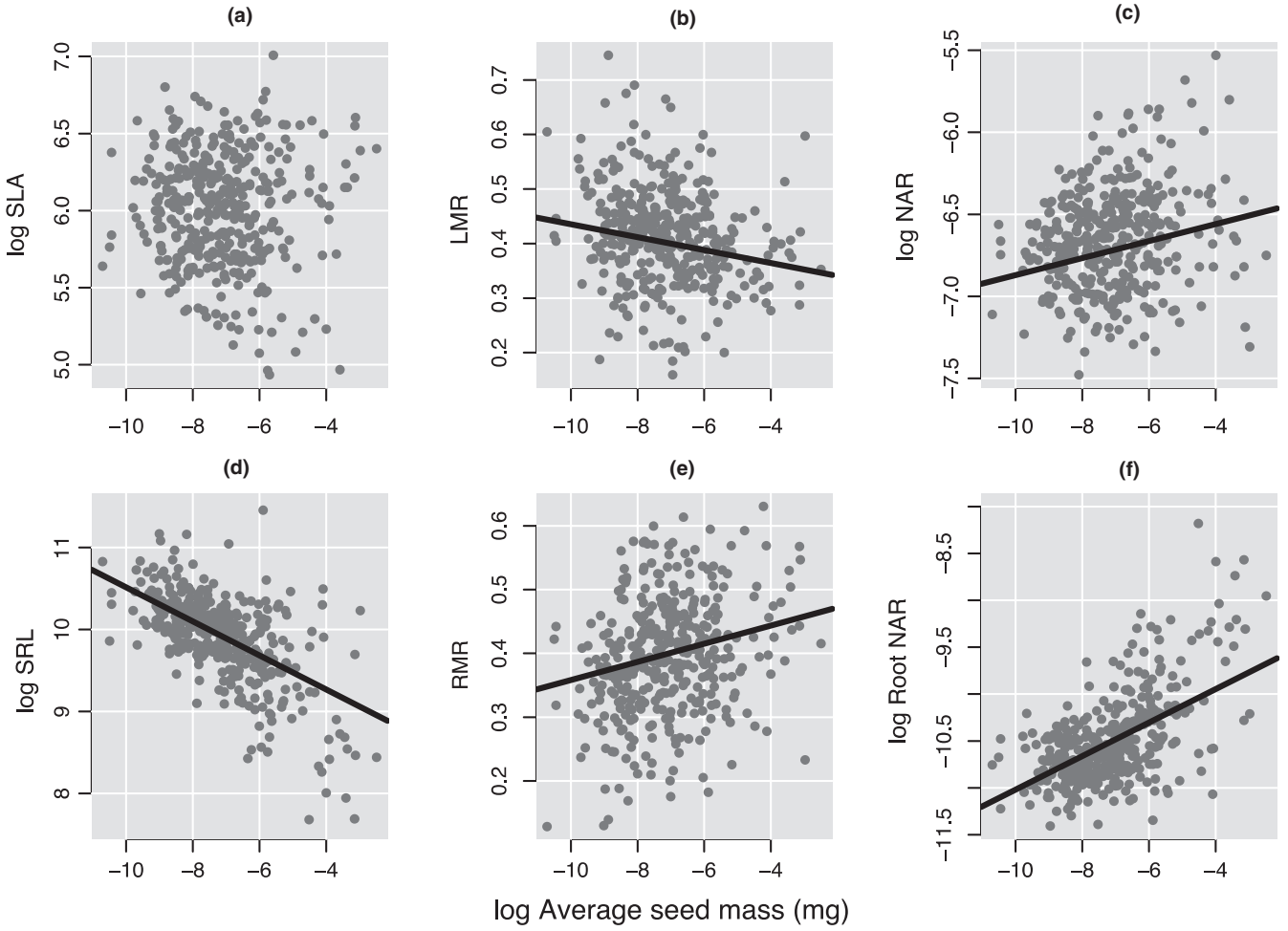

FIGURE 3 Relationships between growth rate components and seed mass across 382 grass species. SLA (in cm^2/g) was unrelated to seed mass (a), but large-seeded species had (b) lower leaf mass ratios (LMR), (c) higher leaf net assimilation rate (leaf NAR; g cm^{-2} day^{-1}), (d) lower specific root lengths (SRL; cm/g), (e) higher root mass ratios (RMR) and (f) higher root net assimilation rates (root NAR; g cm^{-1} day^{-1}) than species with small seeds. Lines shown are extracted from MCMC phylogenetic GLMMs and are significant ($p < 0.05$; model coefficients are given in Table S3 for lead traits and Table S4 for root traits)

size most strongly influences growth rate in species with 'slow-tough' leaf economics. In the functional traits literature, size and leaf economics are usually presented as orthogonal (independent) axes (e.g. Díaz et al., 2016), but here we show that they interact when it comes to growth rate.

By using a size-standardised measure of growth rate, we are able to explore the biological differences between species that do not arise solely from differences in initial size (Turnbull et al., 2012). These methodological considerations and the large number of species studied make this work a substantial advance in our understanding of the seed mass–growth rate relationship. Our grass study species showed significant variation in seed mass (300-fold variation), comparable to that seen in global plant patterns (e.g. the 320-fold decline in mean seed mass between the equator and 60°; Moles et al., 2007), and diversity in traits important for growth and reproduction, making them a suitable taxonomic group in which to study the seed size–growth relationship. The nature of the seed size–SGR relationship for other plant taxa, such as woody species, remains to be seen and should be addressed in the future research. The consistency of the negative seed mass versus RGR relationship across diverse plant groups may lead to similar consistency when growth rate is size standardised. However, this relationship is likely to depend on leaf traits (as found here for grasses) and the duration of seed size effects (e.g. seed reserves in woody species often continue to influence growth rate throughout the seedling and juvenile growth phases; Cornelissen et al., 1996). In addition, the SGR approach may not be suitable for comparisons in other plant groups. The application of this methodology is limited to comparing species that overlap in mass at the ontogenic phase in which they should show their fastest relative growth. For example, woody species can be extremely different in size for the appropriate developmental phase (Cornelissen et al., 1996) that SGR comparison would involve extrapolating size beyond realistic values for part of the species set.

For species with high LDMC, large seeds were associated with faster size-standardised growth rates than small seeds. The larger energy reserves of big seeds do not explain our result as we compared seedlings at a common size. Likewise, the greater depletion of local resources by small-seeded species that take longer to reach

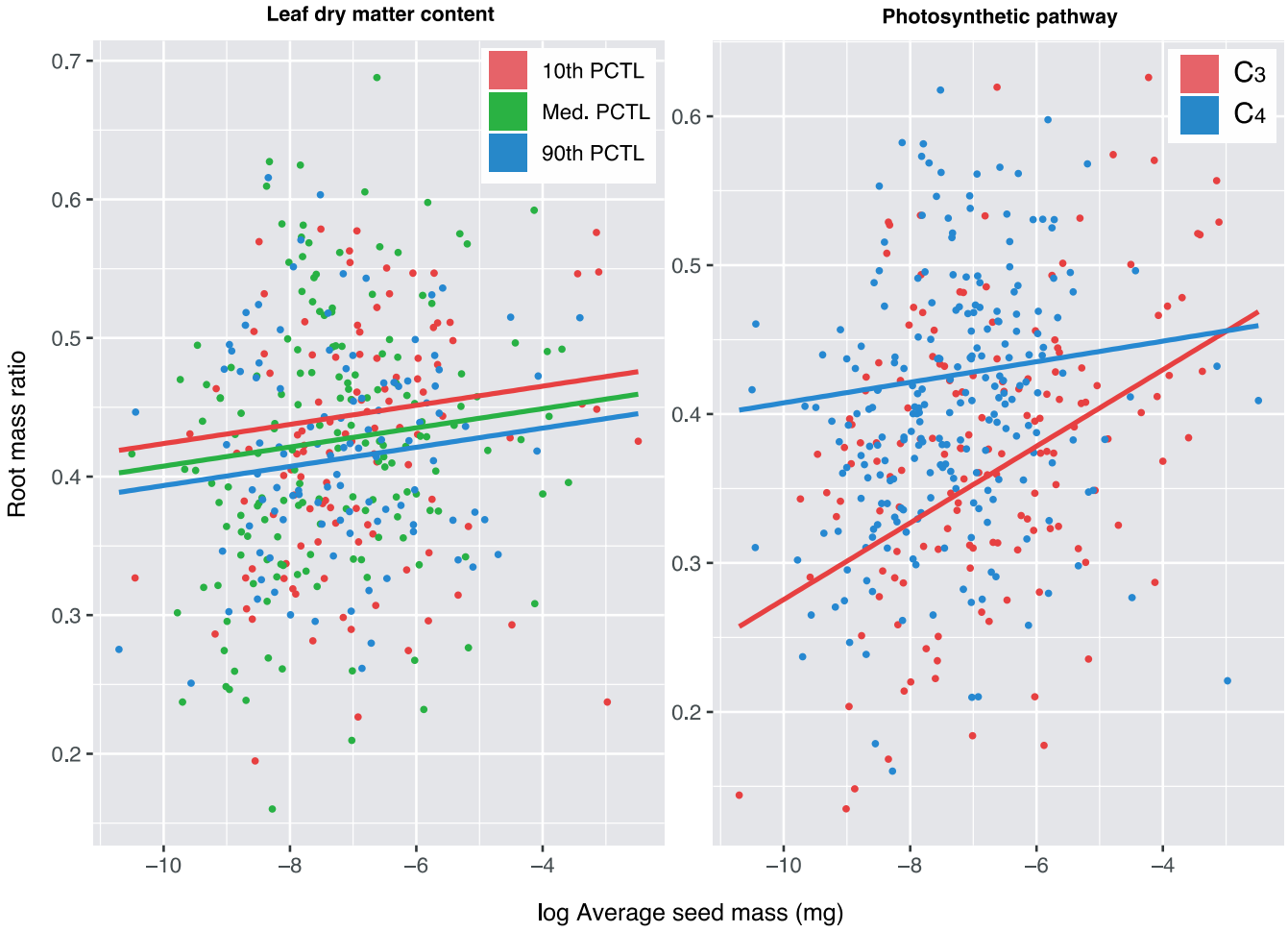

FIGURE 4 Grass species with low leaf dry matter content (left) and the C_4 photosynthetic pathway (right) are associated with high root mass ratios for a given seed mass ($p = 0.023$, $p = 0.01$ respectively). In each partial residual plot, variation due to other variables (e.g. photosynthetic pathway in the left-hand plot) is corrected for to enable clearer interpretation of relationships. Lines shown are extracted from generalised least square linear models, and are calculated for the 10th, median (med.) and 90th percentile (PCTL) of leaf dry matter content in the left-hand plot. Model coefficients are given in Table S6

the common size do not explain our findings, as nutrients were supplied frequently in our experiment. Instead, the advantage of large seeds in high-light conditions was associated with differences in functional traits and biomass allocation. Specifically, large-seeded species invested more in below-ground biomass, as found elsewhere (Baker, 1972; Buckley, 1982; Lloret et al., 1999). When light is non-limiting, other factors become important in driving growth rates. While the plants were watered twice a day, it is probable that they experienced daily water deficits due to the high temperatures and light levels, the freely draining substrate (sand and vermiculite) and the tall, thin pots they were grown in. Therefore, greater investment in root biomass can increase water uptake and thus reduce the negative impact of water limitation, resulting in a growth advantage for large-seeded, high-RMR species. High SRL, which is associated with rapid water uptake (Eissenstat, 1992; Ryser, 1996), was actually negatively associated with seed size—a relationship driven by the thicker roots of large-seeded species (Figure S2). However, the higher RMR of large-seeded species presumably enables a larger soil volume to be explored and greater soil depth to be reached. This water-deficit hypothesis raises the question of how low-LDMC species grow fast regardless of seed size and associated root traits. We found that LDMC significantly influenced the relationship between seed size and root traits (RMR and SRL), with low-LDMC species showing higher RMRs and SRLs than high-LDMC species regardless of seed size (Figure 4; Figure S3). Therefore, the effect of water deficits on growth may be minimised in low-LDMC species through their capacity to rapidly take up water (high RMR and SRL).

With seed mass accounted for, life history and photosynthetic pathway are important predictors of plant growth rate that act independently of seed size. Annual, C_4 species attain faster growth than perennial, C_3 species across the range of seed mass studied. Both the C_4 photosynthetic pathway and annual life history are associated with high SLA values and elevated photosynthetic nitrogen-use efficiency (Atkinson et al., 2016; Garnier et al., 1997). The production of cheaper and more efficient leaves in these species allows more leaf area to be produced for the same biomass investment, resulting in enhanced growth. We also showed that photosynthetic pathway influences the relationship between RMR and seed mass, with C_4

species having higher RMR than C_3 species for all but the very largest seed sizes (Figure 4). Therefore, the C_4 photosynthetic pathway may alleviate the negative effects of water deficits on growth through greater water uptake and storage. This effect occurs independently of LDMC and is particularly pronounced in small-seeded species.

The only ecological and climatic trait predictors of seed mass were domestication status and mean annual precipitation, and the occurrence and direction of these associations are supported by the literature. During the domestication of grasses, large-seeded wild species were subject to selection which resulted in cereal crops having even larger seed sizes (Cunniff et al., 2014; Preece et al., 2017). The relationship with precipitation can be explained by the greater ability of large-seeded species to germinate and establish in dry environments. For example, in neotropical pioneer species, germination was quicker and occurred at lower water potentials with increasing seed mass (Daws et al., 2008). While small-seeded species may be constrained to relatively moist environments due to the risk of drought-induced mortality, larger seeds can emerge from greater soil depths and produce larger, more drought-tolerant plants (Bond et al., 1999; Daws et al., 2007).

This work challenges the 'truism' of small seeds providing an intrinsic growth advantage. Previous work suggests that small seeds benefit in terms of growth and number, prompting questions about the benefits of producing large seeds (Baraloto & Forget, 2007; Maranon & Grubb, 1993; Pacala & Rees, 1998; Poorter et al., 2008; Tilman, 1994). We found, in contrast, that the growth advantage of small-seeded grass species arose from the use of the size-dependent growth metric, RGR. Instead, large seeds provide a growth advantage over small seeds when compared at a common size, because a greater investment in roots resulted in faster growth under the high-light conditions used here. However, large root investment could also be achieved by the possession of other functional traits (low LDMC or C_4 photosynthetic pathway). Such growth rate differences do not necessarily relate to population-scale growth rates: while being small-seeded does not confer an intrinsic growth advantage for an individual, it can result in higher population growth rates and the rapid colonisation of disturbed habitats (Pacala & Rees, 1998; Tilman, 1994; Turnbull et al., 2012). Therefore, because it describes the efficiency of growth, RGR is a useful metric when considering the mechanisms of colonisation, succession and coexistence. It describes how growth rate differs irrespective of why and how this diversity arises. However, SGR is a more appropriate measure when exploring the mechanisms that give rise to interspecific growth rate diversity. The differences in SGR among species associated with seed size are caused by interactions with leaf and root traits, especially allocation to roots (RMR), and leaf and root economics (LDMC and SRL).

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CONFLICT OF INTERESTS

The authors declare no conflict of interests.

AUTHORS' CONTRIBUTIONS

R.R.L.A., M.R. and C.P.O. designed the study; R.R.L.A., E.J.M., C.B. and K.J.S. generated the data; K.J.S., M.R. and C.P.O. analysed and interpreted the data; K.J.S. wrote the manuscript with E.J.M., M.R. and C.P.O. contributing critically to drafts.

DATA AVAILABILITY STATEMENT

Data are deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.ksn02v74j (Simpson et al., 2021). The phylogeny used is published as supplementary data in the study by Atkinson et al., 2016 (Nature Plants: 16038, https://doi.org/10.1038/nplants.2016.38).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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